The female genital structures of *Spanglerogyrus albiventris* Folkerts, 1979. A contribution to the systematic position of the Gyrinidae

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The sclerites and muscles of the ovipositor of *Spanglerogyrus albiventris* Folkerts, 1979 demonstrate a primitive type and status in the Hydradephaga. In contrast to all other Gyrinidae (Gyrinidae s. str.) the ventral tip of the female abdomen is sternum VII and the two gonocoxosterna are well developed as in other Adephaga. In the Gyrinidae s. str. these sclerites are grown together and have been mistakenly regarded as a sternum VIII. Tergum IX is divided in two lateral pole-like sclerites for the evagination of the gonocoxae as in the Gyrinidae s. str., Haliplidae and Noteridae. The muscular system of the ovipositor demonstrates a relationship to the basic design seen within the Coleoptera. In the internal female reproductive system the opening of the vagina, with its short membranous area, is situated between the base of the gonocoxae. These sclerites have a long anteriorly reaching appendage, as in the Orectochilinae, for the insertion of the tergigonocoxal muscle (M 32). The bursa copulatrix, with accessory gland and anterior opening of the long and basally expanded ductus receptaculi, joins the vagina in a far caudate position. The receptaculum seminis is situated to the left of the end of the bursa under which the expanded vagina is located.

The sum of synapomorphies in the Gyrinidae s. str. demonstrates the primitive character of *Spanglerogyrus* (Spanglerogyrinae). The phylogeny of the Gyrinidae is discussed in comparison with other authors.

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Introduction

The phylogenetic position of the Gyrinidae in coleopteran systematics is a subject of continuing debate. An abundance of highly derived characters in this beetle taxon, which must be viewed in conjunction with their adaptation to the Kinon, or specialized habitat of the water-surface, makes it particularly difficult to recognise distinct primitive structural features on which the basal phylogenetic position of this beetle taxon has been justifiably recognised. The remaining Coleoptera, or Hydraphaga, are united by apomorphic characters evident in their phylogenetic relationships. The basal phylogenetic position of the Gyrinidae within the Adephaga and the multiple intrusions of representatives of these beetle groups, recognised through synapomorphies, have been discussed by Kavanaugh (1986) and Beutel & Roughley (1989).

The discovery of *Spanglerogyrus albiventris* Folkerts, 1979, in Alabama, U. S. A. in 1975 and 1979, and its special position within the subfamily Spanglerogyrinae has already been reported and discussed by several authors. Numerous characters, such as the structure of the eyes which are not separated extend to the dorsal and ventral sides of the head but are joined only by a narrow bridge, the clearly

different curvature of the corneas of the ommatidia on both halves of the eye and above all the unshortened middle and hind legs suggests that this combination of characters represents a "missing link" between the (archetype) basic design of the Adephaga and the Gyrinidae s. str. The small body size of *Spanglerogyrus* (max length 2.9 mm) which makes slide preparation of the inner organs very difficult could support the viewpoint cited by Ochs (1926) that small size is a plesiomorphic character in contrast to the opinion of Hatch (1925). The fact that *Spanglerogyrus* has colonised the lotic reaches of streams and rivers contradicts the opinions of these authors since, as is the case with the Orectochilinae − probably the most closely taxon related within the Gyrinidae s. str. − this behavioural pattern may be perceived as a strongly derived character and the Gyrinidae may be presumed to have originated in lentic regions.

A comparative study of the female genitalia and ventral end of the abdomen of *Spanglerogyrus* with those of other related Gyrinidae s. str. (see also Burmeister 1976, 1980) is now appropriate so that a review of the systematic position of the Spanglerogyrinae within the Gyrinidae and Hydradephaga (Adephaga ?, Coleoptera ?) may be given. A clarification of the systematics is thus possible following character analysis of the entire group.

The female genitalia − ovipositor

External anatomy and musculature

In contrast to other genera of the Gyrinidae, the pale ventral side of the abdomen of *Spanglerogyrus* is particularly flat (Fig. 1) and does not have the hair-seam which is characteristic in the Orectochilinae and used for stabilising swimming movements in disturbed water. Ventrally the short and distally extended sternum VII has an arched seam, with a smooth distal portion and on it a median and lateral group of ridges of unknown significance. The posterior border of this sternite, in contrast to all other Gyrinidae, is medially indented with the laterally displaced areas tapering to a point. The tip of the abdomen is formed by the medially overlapping gonocoxasterna which, in contrast to all other Gyrinidae, are not ventromedially fused. This gives the impression of a genuine Sternum VIII (Burmeister
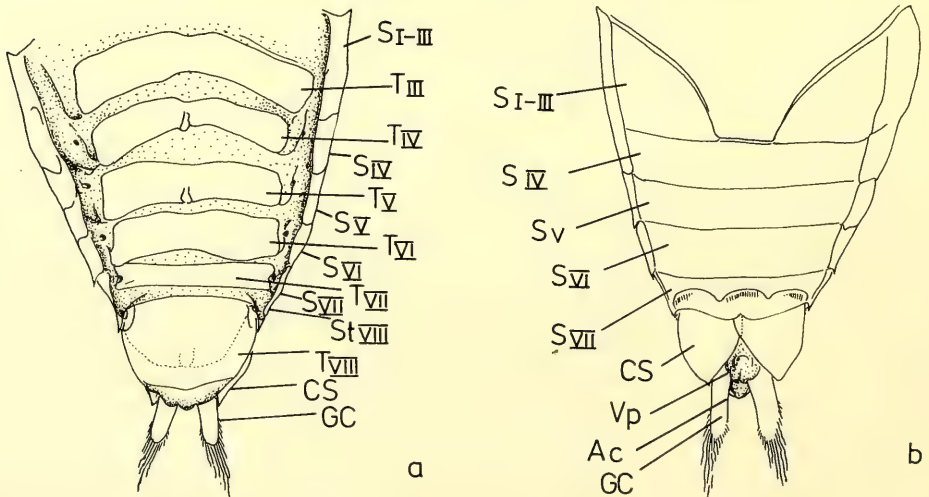

Fig. 1. Dorsal (a) and ventral (b) views of the abdominal tip of female *Spanglerogyrus albiventris* Folkerts, 1979. The ovipositor is partly evaginated.

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1976, 1981) which is, however, absent from the basic coleopteran design (Burmeister 1975). The gono-coxosterna in *Spanglerogyrus* are triangular in shape, distally pointed and dorsally carry an inner row of long sensory setae. Anterolaterally there is a recess, into which the retractor muscles, which origi-nate on the edge of sternum VII, withdrawn along with the dorso-ventral muscles of Tergum VIII. In comparison with the other Hydradephaga, because of the extreme lateral position and slight arching of the sterna, it is not possible to bring the gonocoxosterna to completely a vertical position. In its res-ting position the medially overlapping section (Fig. 1 b, 3) is attached to the anterior edge of the sclerite by a strengthened membranous fold and is bound by a band of muscles.

Dorsally the abdominal tip is bordered by the posteriorly rounded Tergum VIII, under which the anal cone is invaginated distally. The anteriorly attached Tergum VII is particularly strongly sclerotis-ed and is laterally extended downwards where the stigma are fused with the sclerite. Tergite VIII dis-tally has a dense hair-seam whose special function is to trap respiratory air bubbles under the elytra.

Sclerotised gential appendages are absent from Segment VIII (Burmeister 1976, 1981). The vaginal papillae, i. e. the ventral termination of the genital opening, protrude ventrally between the gonocoxo-sterna when evaginated − see below (Fig. 1 b, 2 a). The genital opening, or mouth of the bursa copula-trix, lies between the bases of the Gonocoxae which themselves are adjoined to the genital appendages of Segment IX. In the resting position these projecting appendages are only slightly flattened in *Spanglerogyrus* but display, as in other Gyrinidae, a dense edging of sensory setae distally and on the inner margin which are particularly long towards the apex. Anteromedially the Gonocoxae are drawn out to an apodeme serving as a point for muscle attachment as in the Orectochilinae and Enhydrinae.
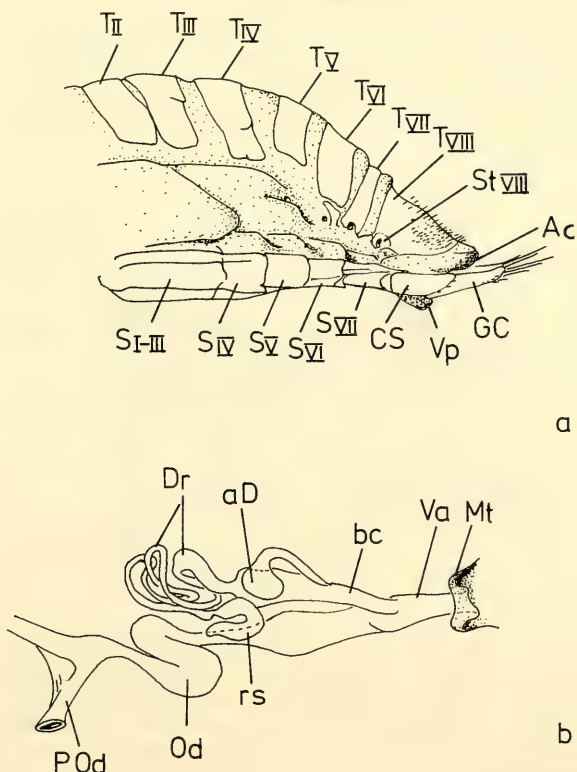

Fig. 2 a.   Lateral view of the abdominal end of *S. albiventris,* Ovipositor partly evaginated.
Fig. 2 b.   Lateral view of the internal female sexual organs and ducts of *S. albiventris.*

The anteriorly slanted remainder of Tergum IX, with which the gonocoxae are flexibly attached to the lateral edge and which have been incorrectly described by Tranda (1968) as "hemisternites" and "paravalvifers" respectively – (see Burmeister 1976), forms a narrow, thin and straight clasp with a lateral orientation (Fig 3, 4). The distal portion of Tergum IX, on the sides of the anal cone in front of the opening of the repugnatorial gland, is absent in *Spanglerogyrus*. In *Gyrinus* these structures are used for muscle anchorage (Burmeister 1976). The dorsal retractor muscle of the anal cone (M24, Burmeister 1976) which also serves as a flexor for the clasp on Tergum IX, is present in *Spanglerogyrus* and is inserted on the inner side of the membrane of the anal cone along with the retractor of the anal cone, M 18, (Fig. 3). The Tergogonocoxal muscles (M 32, M 33), connecting Tergum IX and the Gonocoxae, have a cranial origin on the tip of the aforementioned sclerite (T IX, Fig 3).
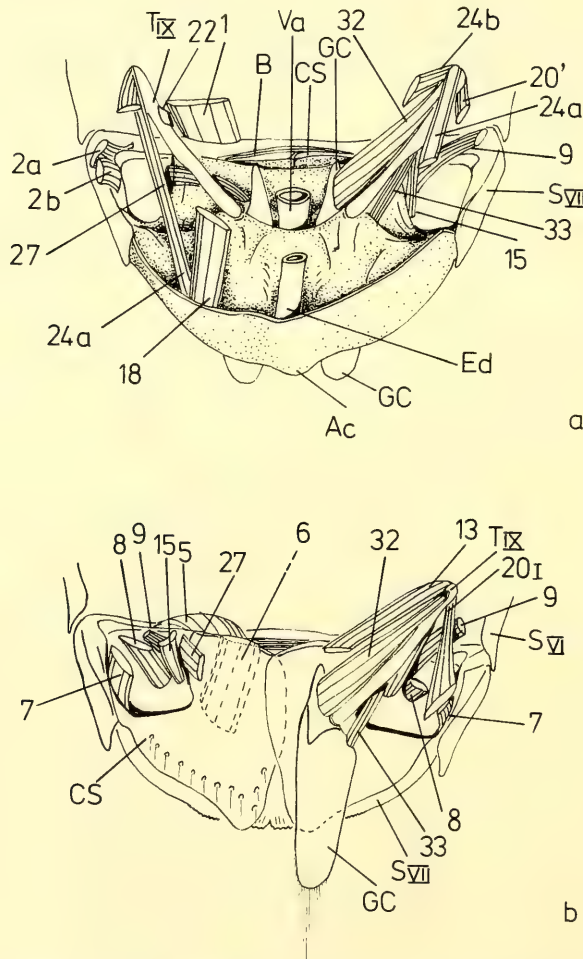

Fig. 3.   Dorsal aspect of the terminal abdominal segments of *S. albiventris*. Ovipositor in resting position. The numerical notation (M 1 – M 33) of the musculature follows Burmeister (1976, 1980). See text for details of the functions and changes of the salient muscles in the course of the phylogenetic history of the Gyrinidae. a) View with Tergum VIII removed showing the infolding membrane and the cranially withdrawn ovipositor sclerite. b) View with Tergum VIII, left half of Tergum IX and left gonocoxa with associated muscles removed. Membrans are not considered. The free outer dorsal surfaces of the gonocoxosterna with the inner sensory setae are clearly visible as is the craniolateral notch (membrane covered) which serves for a muscle attachment.

The protractor muscles of the gonocoxasterna (M 6) extend from the overlapping gonocoxosterna to the anterior border to the posterior inner region of Sternum VII. These muscles are absent in the remaining Gyrinidae (see below). In *Orectogyrus*, there is remained only a slender band on the posterior edge of the gonocoxosternum which arises from the cranial fold (distal border tubercle) of Sternum VII. The ovipositor protractor muscle (M 15), which stretches from the inner margin of the gonocoxosternum to the the anterior part of the sclerite of Tergum IX, is very strong in *Spanglerogyrus* and springs from the anterolateral notch of the gonocoxosternum (Fig. 3). In the Orectochilinae this muscle is particularly flat and arises from the posterior overlapping portion of the medially coalesced Gonocoxosterna.

In contrast to the other Gyrinidae, in *Spanglerogyrus* the ventral region of the genital opening, directly under the base of the gonocoxite, is not tapered to a point but is only turned forwards as a swollen ventral membrane. Sclerotised parts of genital appendage VIII are not present, nor is any evidence for a formerly existing vaginal musculature, which could have a use for pulling in a distal direction or dilation of the genital opening.

Internal female genital organs

The internal genital organs open to the exterior between the basal parts of the Gonocoxae. Here the vaginal opening extends in front of a narrow folded membranous pouch which can be rolled down like the finger of a glove, whereby the sexual opening becomes turned towards the posterior end. In the vaginal tube there is a widening into which the unpaired oviduct opens ventrally. This is very short and like both of the branched paired oviducts does not exhibit the muscle layers which are characteristic of the vagina (Fig. 4, 2 b). The paired oviducts, which lead from the paired ovaries, are attached by a flexible band around the region where they meet before leading into the unpaired oviduct. The vaginal sclerites ("vaginal teeth", Brinck 1955), as seen in the Gyrinini, are apparently absent.
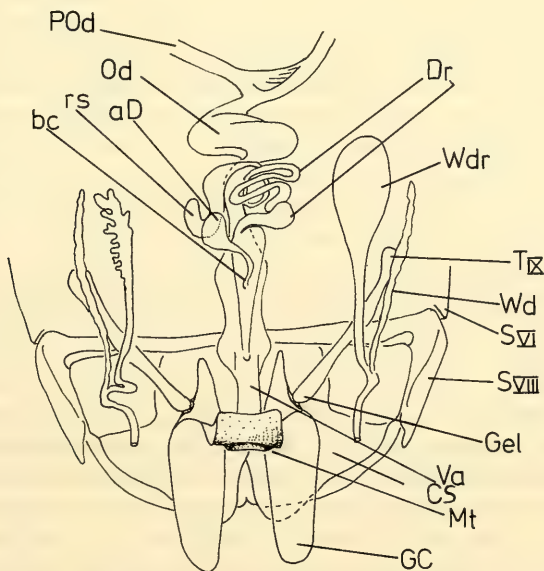

Fig. 4. Dorsal view of the ovipositor (resting position), showing the internal sexual organs and the lateral repugnatorial gland (left repugnatorial gland reservoir (Wdr.)) without liquid.

Like in the Orectochilinae *(Orectogyrus* s. Brinck 1955) the bursa couplatrix opens dorsally into the vagina, some distance caudally and around the region of the gonocoxal apophyses. In the remaining Gyrinidae the bursa copulatrix appears only as an anterior appendage of the vagina in the region where the unpaired oviduct opens. The ductus receptaculi is attached to the bursa copulatrix which is also identifiable by the musculature of its wall. The ductus is enlarged (gland tissue?) directly before it merges with the bursa while anteriorly it appears as a narrow much coiled tube with a distinctly widened apical portion which is clearly the receptaculum seminis. In his interpretation of these particular sections Brinck (1955) used a confusing terminology which ran contrary to the basic design of the internal genital organs (Heberdey 1931). The receptaculum seminis (sensu Brinck 1955), one of the integral structures of the bursa copulatrix present in *Orectogyrus,* is absent in *Spanglerogyrus.* As in the Orectochilinae, the dorsal sections of the sperm reservoirs (the bursa copulatrix, ductus recapticuli and receptaculum seminis) are separated from the ventral parts (vagina, unpaired oviduct, paired oviducts) i. e. the exit, which serves primarily for oviposition and is situated some distance posteriorly. A small roundish accessory gland opens dorsolaterally (right side) in the bursa copulatrix (Fig. 2 b, 4). The relative positions and state of extension of the individual organs are dependent on the development stage and sexual maturity of the female.

The Systematic Position of *Spanglerogyros* Folkerts, 1979

The systematic position of members of the family Gyrinidae, as interpreted by numerous recognisable synapomorphies, remains contentious and the variously constructed phylogenetic trees contradict each other extensively.

The basal phylogenetic position of the Gyrinidae has been discussed by Beutel and Roughley (1989). As true Adephaga, the Gyrinidae have been placed opposite the remaining representatives of this coleopteran group substantiated by synapomorphies within the latter. Bradley (1947) discussed the possibility that the Gyrinidae are opposite all other Coleoptera and are more closely related to the Megaloptera on the basis of larval characters. These characters have also lead to the false conclusion that the well known larva of *Permosialis* (Sharov, 1953), from the Permian presumably belongs to the Gyrinidae, or a basic group (Beutel & Roughley 1989). The occurrence of clearly different water-beetle larvae like Gyrinidae already in the Permian has induced the primitive status of this taxon. However , Crowson's (1975) supposition that this beetle taxon branched off from the evolutionary line in the Triassic can not be proved by the lack of fossil evidence. Based on the available fossil evidence Kavanaugh (1986) has shown that the Hydradephaga, with the exception of the Haliplidae, forms a composite group. From this it is clear that the related families (Hygrobiidae, Noteridae, Amphizoidae, Haliplidae) are not represented in the fossil evidence of the Mesozoic.

The symmetrical arrangement of the penis and the lateral parameres (also symmetrical) in the body interior serve as evidence for a basal phylogenetic placement of the Gyrinidae — a situation also seen in the Cupedidae (see also Edwards 1953). However, the relative positions of the individual sclerotised elements, particularly the phallobase, has a different expression and arrangement in the Gyrinidae.

If there is one stem species, or a lineage with an unknown number of various representative beetle groups (monophylous) of the Hydradephaga (Bell 1967, Burmeister 1976, Baehr 1979, Ruhnau 1986, Beutel & Belcaceme 1986), thus the position of the Gyrinidae becomes relatively straightforward in relation to true inhabitants of semiaquatic (kinon) habitats and their consequential adaptive characters (Omer-Copper 1934). The sister-group relationships between the Gyrinidae and the remaining Hydradephaga have been postulated by Boeving & Craighead (1931), Bell (1966), Baehr (1979) and Evans (1985).

Within the Hydradephaga, assuming that the Gyrinidae actually belong to this group, the monophyly of the Amphizoidae, Hygrobiidae and Dytiscidae was first established through synapomor-
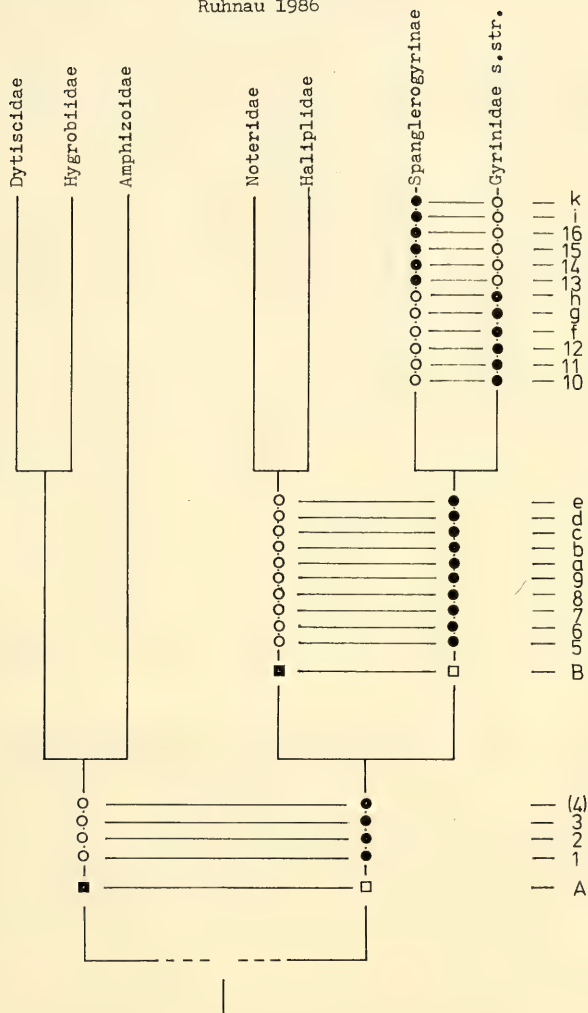
Fig. 5.   Cladogram of the Hydradephaga with special reference to the Gyrinidae (see text for list of characters. The characters A and B correspond to data of Burmeister (1976) and Ruhnau (1986). o plesiomorph, ● apomorph. 1—16: characters of the female genital structures; a—k: other morphological features.

phies by Burmeister (1976) — a viewpoint confirmed by the works of Ruhnau (1986), Beutel (1986), Burmeister (1988) and Dettner (1989). Within the remaining families there is also an obvious uniformity in the Haliplidae and Noteridae (Burmeister 1976, Baehr 1979, Ruhnau 1986) which Burmeister (1976) and Ruhnau (1986) have placed opposite the Gyrinidae as as sister-groups (Fig. 5, dendrogram).

In the bifunctional system of organs for oviposition and copulation with both sperm absorbtion and transfer capacity, the cranial tip of the median separated part of the original Tergum IX and its function as a support for the gonocoxae with the median genital opening is conspicuous in the Haliplidae,
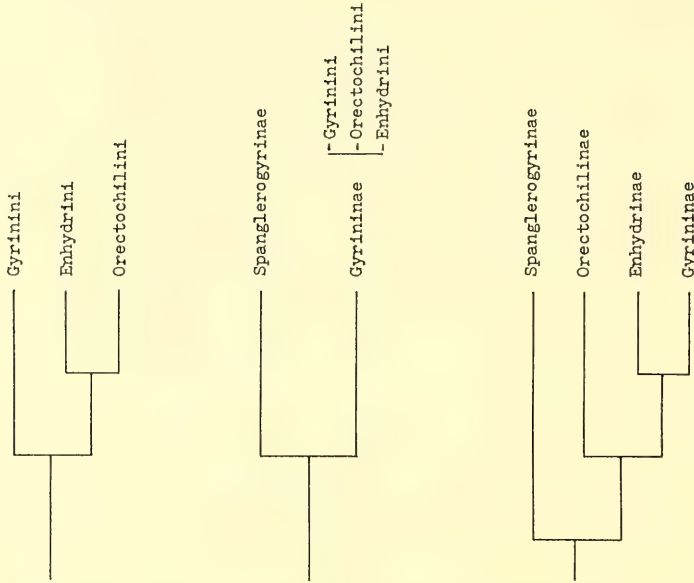
Fig. 6.   Possible relationships within the Gyrinidae according to different authors.

Noteridae and Gyrinidae. A bare evaginated papilla or membranous pouch is not present in representatives of these taxa thus they have to actively search for a niche to deposit the egg. Burmeister (1976) and Ruhnau (1986) have given a total of nine synapomorphies in support of the hypothesis that the Gyrinidae and Noteridae +Haliplidae form a monophyletic group.

Synapomorphies recognised by Burmeister (1976) from the character analysis of the female genitalia of the Gyrinidae + *Spanglerogyrus* and the Noteridae + Haliplidae remain unchanged in this analysis. New synapomorphic characters of the ovipositor are indicated by numerals, others by letters (Fig. 5.).

1) Tergum IX divided, always formed as cranial sclerites.
2) Tergogonocoxal muscles (M 32, M 33) arise anteriorly on the inner surface of tergal clasp (T IX)
   In *Spanglerogyrus* M 33 is displaced to the underside of tergal clasp IX (Fig. 3).
3) Tergal protractors (M 15) of T IX − halves arise from the inner surface of the gonocoxosterna and are inserted cranially on the anterior border of each half of the tergum.
   In *Spanglerogyrus* the origin of these muscles is displaced laterally to the membrane-covered corner of the gonocoxosterna.
4) The dilator muscle of the vaginal opening (M 22, Burmeister 1976) arises anteriorly from the tergal clasp (T IX) and also functions as a retractor for the ventral membrane of the anal cone.
   In the Haliplidae this muscle is reduced, as in *Spanglerogyrus,* where a flat band is retained to the inner surfaceover the vaginal opening (see also Burmeister 1976).

Since the larva of *Spanglerogyrus* is not known, a comparison with the character analysis of Ruhnau (1986) is not possible.

The autapomorphies of the Gyrinidae alongside the characters of the external anatomy, also in the region of the ovipositor, must be changed and defined in more detail (compare Burmeister 1976, Folkerts 1979).

5) Gonocoxosterna overlap ventromedially and are bound by a stretched membrane or else grow together.
   This progressive fusion and functional simplification is noticable in the relative proportions of the gonocoxosterna in *Spanglerogyrus*. The presence of a sternum VIII in *Triadogyrus* Ponomarenko (Ponomarenko 1977) raises questions about the status of this fossil genus from the Triassic.
6) Membrane of the anal cone is not turned inwards ventrally towards the tergal clasp (T IX) over the genital opening.
7) Gonocoxae and flexibly connected tergal halves IX horizontal, the halves angular laterally.
8) Tergogonocoxal muscles (M 32, M 33) serve to spread and draw together the gonocoxae and thereby also the genital opening.
9) Dilators of the vagina, with origin on the inner surfaces of the gonocoxae, absent (reduction character!)

Along with these characters of the female genitalia additional external features may be referred to which are derived in Gyrinidae s. str. and *Spanglerogyrus*.

a) Eyes always divided into two functional units, curvature of the omatidial lenses in each half clearly different.
b) Antennae markedly shortened, pedicel with long setae on lateral border — horizontally placed (in relation to the water surface).
c) Mesosternum very extensive, flat; mesocoxae displaced backwards, the rere edge drawn out from the medioposterior to a laterocranial position (see Hatch 1925, Matsuda 1970, Beutel & Roughley 1989).
d) Prosternal process short, does not reach the rere edge of the procoxa (considered by Beutel & Roughley 1989 as a plesiomorph feature!), procoxa with a distal groove.
e) Sterno-gonocoxal articulation of the prothorax displaced laterally (restriction of movement towards ventral).

An evaluation of the characters cited by Baehr (1979) and Beutel & Roughley (1989) — synapomorphies of representatives of the Gyrinidae with respect to other families of the Adephaga or Hydradephaga — is in many cases not possible, especially since the opinions expressed by the authors contradict each other and apparently the argumentation is directed to one opinion, thus complicating the construction of a phylogenetic hypothesis. The differing viewpoints were insufficiently discussed by Beutel & Roughley (1989).

The basal position of *Spanglerogyrus* in Gyrinid systematics is documented by the following synapomorphies of the Enhydrinae, Orectochilinae and Gyrininae, i. e. the Gyrinidae s. str. (excluding *Spanglerogyrus*) (plesiomorph in *Spanglerogyrus*).

10. Gonocoxosterna coalesced ventromedially, and distally forming the ventral abdominal tip. An invagination of these unpaired sclerites does not appear to be very likely. These fused gonocoxae have been falsely homologised to a sternum VIII!
11. Protractor (M 6) of Gonocoxosterna (GC) absent.
12. Adductor (M 42) of gonocoxae directly binds both sclerotised elements of these tactile organs anteriorly (see Burmeister 1976).

Additional characters of the external anatomy: Synapomorphies of the Gyrinidae excluding *Spanglerogyrus* (see Folkerts 1979, Kavanaugh 1986, Beutel & Roughley 1989).

f) Eyes clearly separated, partly extended to the upper and lower sides.
g) Adhesive pad of the anterior male tarsi displaced laterally. Male fore legs clearly longer than those in females.
   In the male *Spanglerogyrus* the adhesive pads of the anterior tarsi are somewhat turned towards the ventral side.
h) Meso- and metatarsus much shortened, flat and plate-like.

The autapomorphies of the monospecific genus *Spanglerogyrus* Folkerts, 1979 can only be understood in the context of the position of this species in relation to other members of the family Gyrinidae. Moreover, possibilities of prior branching in extinct lineages of the Coleoptera, specifically in the Adephaga and Hydradephaga, are insufficiently known (Kavanaugh 1986) so that a comparison of plesiomorphies and apomorphies is especially difficult. Just as in the Gyrinidae, with their specialised and extreme lifestyle on the air-water interface (Omer-Copper 1934) — unique insects that live on the surface tension of water, the underside is moistened — symplesiomorphies are frequently superimpos-

ed on apomorphies, so that the starting point is hardly recognisable. Features seen on *Spanglerogyrus* have brought a "glimmer of light" to the "shadow" covering this part of the phylogenetic history. Its autapomorphies, as follow below, are hypothetical and are based on current knowledge only.

13. Tergum VII heavily sclerotised and drawn downwards at the sides (the stigmata are integrated).
14. Sternum VII notched distally on the median border and underneath has wavy ridges and an area of setae on the rim; each posterolateral corner is drawn to a point.
15. Vaginal field, under the genital opening, reduced as also is the remainer of the genital appendage VIII and its insertion musculature.
16. Gonocoxosterna dorsally only on the latero-cranial corner with a non-membranous opening as a muscle anchorage point. The inner surface also covered with sensory setae.
    The overlapping and coalescence of the gonocoxosterna may be considered as a precursor for their fusion. (Plesiomorph within the group Gyrinidae s. str. + *Spanglerogynus*, see above).

There are other autapomorphies in *Spanglerogyrus* apart from those of the female genitalia and abdominal tip.

i) Meso- and metatibia drawn into a long ridge which nearly reaches the point of the tarsus (lying parallel).
k) A deep notch is present on both sides of the head at the base of the antennae and in front of the eyes.
    The jumping ability of *Spanglerogyrus albiventris* Folkerts may also be viewed as a specialization (Folkerts 1979, Steiner & Anderson 1981), especially when a similar behaviour is encountered in the Laccophilinae within the Dytiscidae.

The similarities to be seen in the female genitalia of *Spanglerogyrus* and in the Orectochilinae (Gyrinidae), are particularly striking but however are now without value in the phylogenetic context.

– Gonocoxae extended longitudinally, entire border hairy.
– Tergite halves (T IX) strongly articulated laterally (tergogonocoxal articulation), cranial process of the gonocoxa arises directly from the joint. Such a process is also present in the Enhydrinae which, however, is formed as the cranial tip of the gonocoxae.
– The dorsal side is much arched (adaptation to life in flowing waters – lotic reaches)
– Elytra hairy. In *Spanglerogyrus* the hair cover is without a shagreen area from the front to the rere of the elytra. This clear surface is reminiscent of that seen in *Orectogyrus* whereas in *Orectochilus* the elytra are completely hairy.
– A tendency to orthognathy, the mouth parts are directed more downwards than anteriorly.
– The female gonocoxasterna are not completely fused posteriorly (with an occasional very short median notch).
– The gonocoxosterna are partly withdrawn into segment VIII (invagination) which is not possible in other Gyrinidae (Enhydrinae, Gyrininae). This is all the more surprising in the Orectochilinae since the ventromedian keel of hair is formed (segment VII and VIII), particularly on the coalesced gonocoxasterna which are also drawn into the segment adding to the difficulty in the evaginated position of arranging the hairs which obviously serve as a stabilising keel.

Discussion

If the phylogenetic hypothesis for the Gyrinidae is correct, i. e. that *Spanglerogyrus*, or rather Spanglerogyrinae, is the sister group of all remaining Gyrinidae (s. str., Figs 6, 5) thus the characters of *Spanglerogyrus* common to part of the Gyrinidae s. str. are considered as plesiomorphic. The occurrence of common characters within the Gyrinidae s. str. indicating a modification of the plesiomorphic condition is thus concerned with syn. apomorphies, which could be the basis of the monophyly of the group, or else is concerned with convergence.

In relation to the Gyrinidae s. str. it is on the basis of the morphology of *Spanglerogyrus* that the Orectochilinae, with plesiomorphic characters, stand opposite the Enhydrinae + Gyrininae with synapomorphies. Until now the Orectochilinae have been considered the most derived group (Hatch 1925) not least because of their mode of life in lotic waters. However, these lotic reaches can also be

regarded as original habitats as evidenced by representatives of other insect groups. Moreover, members of the Enhydrinae, *(Dineutes, Porrhorrhynchus)* also inhabit flowing water but have however, a totally different shape (wide, flat on top, elytra with long points to push aside the waves in the current, different position in the water). Hatch (1925) combined the Orectochilinae with the Enhydrinae and placed them opposite the Gyrininae since in both the galea is reduced (a galea is present in *Spanglerogyrus!*). The coppotentorium has been lost in the Enhydrinae and Gyrininae. Hatch (1925) gave the following characters as original which may be contrasted to the situation in *Spanglerogyrus:*

- antennal flagellum nine-jointed
- scutellum visible
- galea present
- hair absent from the elytra!
- elytra rounded! (different in *Spanglerogyrus*)
- body large!
- male genital lobes (parameres) broad and flat! (! – aberrant in *Spanglerogyrus*)

Ochs (1926) presumed that a small body size is primitive which could have been apparent through the tendencies seen in the Dytiscidae. In the females it is particularly noticable that the plesiomorphic ovipositor (apomorphic status: saw, knife for cutting plant tissue) used in searching for egg niches on the water surface (oxygen provision) is not developed to the extreme which suits smaller species. The interrelationships within the Gyrinidae s. str cannot be prepared hastily, Fig. 5 depicts a trend only.

The internal female sexual organs of *Spanglerogyrus* display a clear affinity with those of the Orectochilinae. This is also not a definitive statement. It follows from this postulation that the caudal separation of the vagina and bursa copulatrix, from the dorsally displaced receptaculum seminis associated with the ductus receptaculi, must represent an original situation (see above). The coiling of the long passage – ductus receptaculi – with the scarcely discernable recapticulum seminis is reminiscent of the relative positioning of these structures in the other Hydradephaga (Burmeister 1976, 1980, 1989). The accessory gland that opens dorsally into the last section of the ductus receptaculi has not been observed previously in this position. The extended terminal section of this passage for semen may also be defined as a dorsal passage of the vagina or connecting bursa copulatrix respectively. Thereby the impression emerges that this distal separation of the bifunctional uniformity of the female genital structures has already reached a condition of a double sexual opening – convergence ? (Burmeister 1976, 1980). The descriptions given by Brinck (1955) of the position of the receptaculum seminis in the final part of the vagina (ventral!) or the vagina and bursa copulatrix are certainly wrong and refer to strong membrane or sclerotised parts of the inner cuticle. The formation of the remaining parts of the internal sexual organs in *Spanglerogyrus* exhibit so many peculiarities and to such a degree that a relationship of the female genital openings to other organ systems is still not yet possible.

Acknowledgements

Abbreviations

Ac	Anal cone		CS	Gonocoxosternum
aD	Accessory gland		Dr	Ductus receptaculi
B	flexible band between		Ed	end of intestine -rectum
	both gonocoxosterna		GC	Gonocoxa
bc	Bursa copulatrix		GeL	Tergogonocoxal articulation

Mt	Membranous pouch	Va	—	Vagina
Od	Unpaired oviduct	Vp	—	Vaginal papilla
pOd	paired oviduct	Wd	—	repugnatorial gland
rs	Receptaculum seminis	Wdr	—	repugnatorial gland
S	Sternum (I—VII)			reservoir
St	— Stigma (I—VIII)	1—33		Musculature of female
T	— Tergum (I—VIII)			genital segments
(T IX	— Tergum halves IX)			

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